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Plantation management history and coarse woody debris characteristics influence the diversity of saproxylic beetles associated with Chinese cedar in Tianmushan, Zhejiang, East China

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Abstract: Unreasonable forest management has been proposed as an important causation for the decline of saproxylic beetle diversity. In subtropical regions of China, plantation forests have been widely established to replace natural forests with high diversity. However, our knowledge about the impact of these plantation forests on saproxylic beetle diversity is still very poor. In this study, we compared the composition and diversity of saproxylic beetle assemblages associated with snags of Chinese cedar (*Cryptomeria fortunei*) in young cedar plantation (YPF) (30 - 40 year), mature cedar plantation (MPF) (80 - 100 year), and semi-natural mixed forests (SNMF) (>200 year) in Tianmushan Nature Reserve, Zhejiang province. The results showed that the number of saproxylic beetle individuals was significantly higher in SNMF (97.4 ± 66.7) (mean ± *SD*) than in YPF (39.9 ± 16.3) and MPF (21.9 ± 5.9). However, no significant difference in species richness was found between SNMF (27.9 ± 11.2) and YPF (24.1 ± 3.7). In contrast, the numbers of species and individuals were significantly higher in YPF than in MPF ($P < 0.05$). Both species richness and abundance were significantly related to the volume of coarse woody debris (CWD) in surveyed plots ($P < 0.05$). The canonical correspondence analysis and multi-response permutation procedure analysis confirmed that the saproxylic beetle assemblages were significantly different between forest types ($P < 0.001$). The diameter of sampled snags, CWD diameter and amount, and canopy cover in plots had significant effects on species composition ($P < 0.05$). Analysis of trophic composition also indicated that mycetophagous species were significantly more abundant in SNMF than in plantation forests ($P < 0.001$). The results suggest that improving quantity and quality of CWD habitats in cedar plantations may increase species richness of saproxylic beetles, but the diversity of saproxylic beetles in these plantations may decline in later succession stage. Furthermore, saproxylic beetle assemblages in cedar plantations may remain distinct from those in natural forests.

Key words: Saproxylic beetles; species diversity; Chinese cedar; management history; plantation forest; coarse woody debris; Tianmushan

1 INTRODUCTION

Saproxylic beetles are an important Coleoptera group that depends on dead wood (or decaying wood) or organisms associated with dead wood (such as fungi) for their development in part of their life cycle (Speight, 1989). They not only play an important role in initiating and promoting the decay process of coarse woody materials (Reichle, 1977; Hammond *et al.*, 2001), but also comprise a considerable proportion of species diversity of forest invertebrate fauna (Grove, 2002a). For instance, in Finland it is estimated that 4 000 - 5 000 forest-dwelling species are saproxylic species, amongst them about 800 species are beetles (Siitonen, 2001). In a German forest, 56% of forest beetle species are considered saproxylic (Köhler, 2000).

The diversity of saproxylic beetles greatly depends on the qualities and availabilities of dead wood habitats, thus is highly susceptible to the reduction in dead wood amount caused by intensive forest management (Siitonen, 2001; Grove, 2002a; McGeoch *et al.*, 2007; Davies *et al.*, 2008). In the

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past two decades, the conservation of saproxylic beetles has caused special concerns in temperate forests of the Northern Hemisphere. It has been proposed that the species number of saproxylic beetles is greatly lower in managed forests than in old-growth forest (Chandler, 1991; Martikainen *et al.*, 2000; Sippola *et al.*, 2002; Hammond *et al.*, 2004; Dollin *et al.*, 2008). Many rare or red-listed saproxylic beetle species are found more common in old growth forests than in managed forests (Sippola *et al.*, 2002; Similä *et al.*, 2003; Hammond *et al.*, 2004). Accordingly, it has also been suggested that the saproxylic beetle assemblages are greatly different between managed and old-growth forests with almost no overlap (Martikainen *et al.*, 2000). Some dead wood characteristics structured by forest management have been proposed to explain differences in species composition of saproxylic beetles, such as degree of sun exposure (Lindhe *et al.*, 2005; Brunet and Isacsson, 2009b), left dead wood position (felled and standing) (Jonsell and Weslien, 2003), tree species and diameter size of logging residues (Jonsell *et al.*, 2007).

Besides in temperate forests, the protection of saproxylic fauna and their habitats has also caused growing concerns in tropical forests of Australia and Africa (Grove, 2002b; Lachat *et al.*, 2006; Gates *et al.*, 2011). However, relevant knowledge is still very poor in other regions, though thousands of saproxylic species there may be at risk of extinction as their equivalents in Europe.

Take China for example, the natural forest had been seriously destroyed before 1949. As an important measurement of restoring forest area, plantation forests in China experienced a rapid increase in percentage from 4.5% to 33.8% in the half past century (Zhang, 2006). According to the 6th national forest resource inventory (SFA, 2005), the plantation forest area in China already reached 53 million ha in 2003. This conversion of natural forests to plantation forests is expected to greatly influence the diversity and composition of saproxylic invertebrate assemblages because most of these plantation forests are extreme examples of intensive forest management, and characteristics of even-aged monocultures, poor vertical structure and low spatial heterogeneity. The negative effects of plantation forests are probably more severe on saproxylic fauna living in subtropical forests, where the natural broadleaved forests with high diversity have been dramatically cleared and substituted by uniform plantation forests and degraded secondary forests (Chen and Chen, 1995). However, there have been no published studies on the effects of forest plantation on diversity of saproxylic fauna in subtropical forests of China. This condition is far behind the urgent conservation needs of saproxylic diversity in these regions.

In this study, we used the saproxylic beetles associated with snags of Chinese cedar (*Cryptomeria fortunei*) as indicators to assess the influence of plantation forests on the saproxylic biodiversity in subtropical forests. Chinese cedar is not only one of the most widely planted commercial coniferous species in China and East Asia, but also a dominated tree species in natural subtropical forests. It can be distinctly distinguished from other tree species by its huge body shape (maximal diameter breast height: ca. 2.4 m; height: ca. 40 m). The dead wood of Chinese cedar with huge diameter may take decades more to break down, and thus may provide more heterogeneous habitats for specialist species. Nevertheless, on the other hand, monospecific plantations of Chinese cedar, which is the strongest competitors for most broadleaved tree species, probably slow down the natural regeneration and ecological succession of degraded subtropical sites, and thus probably have long-term and unexpected effects on saproxylic fauna in these sites. Our aim in this study was (i) to investigate the differences in assemblage composition and diversity of saproxylic beetles associated with Chinese cedar between plantation (young and mature) and semi-natural forest, (ii) to identify the characteristics of coarse woody debris (CWD) attribute these differences in different forest types, and (iii) to assess the role of cedar plantations with different management history in maintaining the saproxylic diversity in subtropical forests of China. Our study will contribute to a baseline understanding of what is happening on saproxylic fauna in subtropical forests of China and how the present forest management in China should be improved to conserve saproxylic biodiversity.

2 MATERIALS AND METHODS

2.1 Study forests

This study was conducted in Tianmushan National Nature Reserve, Zhejiang Province, East China (119°23′47″ – 119°28′27″E, 30°18′30″ – 30°24′55″N). This area is near the north border of mid-subtropical zone with mean annual temperature 8.8 – 14.8℃ and mean annual precipitation 1 390 – 1 870 mm. This nature reserve has an area of 4 284 ha, of which 88% areas are covered with forest. In these forests, about 20% areas are natural and semi-

natural forests, which are mainly distributed along a range of elevation 400 – 1 300 m on the south slope of West Tianmushan. Especially, this nature reserve preserves the largest primeval population of Chinese cedar in the world (Wang *et al.*, 2007).

Except for natural and semi-natural forests, there is still a certain amount of productive plantation forests in this nature reserve. Most of these plantations were planted before nature reserve established in 1975. Chinese cedar and other two conifer species (*Cunninghamia lanceolata* and *Pinus massoniana*) are three most common tree species in these plantations. However, only Chinese cedar plantation has a varied management history over 100 years.

In this study three forest stands along the south slope of Tianmushan in nature reserve were respectively selected to represent three forest types with different management history, and the direct distance between individual stands was at least 1 km:

1) Young cedar plantation forest (YPF, ca. 9 hm^2): This stand is located at the foot of West Tianmushan mountain (elevation: 360 – 470 m), and near to the southwest border of nature reserve. Chinese cedars in this stand were planted ca. 30 – 40 years ago and never cut before. Except for Chinese cedar, only few *Cu. lanceolata* were mixed planted (< 10%).

2) Mature cedar plantation forest (MPF, ca. 4 hm^2): This stand is also located at the foot of West Tianmushan mountain (elevation: 370 – 480 m), but very near to the southeast border of nature reserve. Chinese cedars were planted ca. 80 – 100 years ago and never cut before. Chinese cedar is still the most dominated species in this stand (ca. 70%), but some broad-leaved tree species such as *Quercus acutissima*, *Carya cathayensis* and *Liquidambar formosana* are also present in this forest for the reason of natural succession.

3) Semi-natural mixed forest (SNMF): This stand is located on the western side of sleepy valley on the south slope of West Tianmushan (elevation: 490 – 550 m). Chinese cedars in this stand were planted hundreds of years ago (>200 year). Since then this stand was less disturbed by anthropogenic activities and could be approximatively regarded as in semi-natural status. Except for Chinese cedar, this stand characterized with dominant broadleaved tree species with high diversity such as *Cyclobalanopsis glauca*, *Cyclobalanopsis mysinaefolia*, *Litsea coreana*, *Phoebe sheareri* and *Phoebe chekiangensis* so on.

2.2 Beetle sampling and identification

In April 2010, we surveyed the Chinese cedar snags in three studied stands. We recorded the decaying stage, diameter and height of encountering snags. In each stand, all snags with DBH >10 cm, height > 1.5 m and meeting the medial decay standard (equal to stage II in Wu *et al.*, 2008) were specially marked. Amongst them, ten snags in each stand were randomly selected for the following beetle sampling. The direct distances between any two adjacent selected snags were at least >50 m.

To sample saproxylic beetles associated with these selected cedar snags, the flight intercept trap (FIT) was employed. The trap consisted of a transparent plastic pane (10 cm × 20 cm) and attached perpendicular to southern side of snag at the height of 1.3 m. Below the FIT, a plastic collecting funnel (top opening diameter: 15 cm) was attached and connected with a removable bottle (capacity: 500 mL; caliber: 5.5 cm) 1/4 filled with 50% ethylene glycol and a few drops of detergent. These small traps closely attached on dead snags were recommended to reduce the random catching of beetles less associated with deadwood habitats in many studies (Gibb *et al.*, 2006; Brunet and Isacsson, 2009a, 2009b).

A total of 30 FITs were settled, but 5 of them were frequently destroyed for squirrel biting and other unknown reasons. Thus, only the data from 25 FITs were included in the final analysis (YPF, n = 7; MPF, n = 8; SNMF, n = 10). These traps operated from April to October in 2010. Beetles were separated from each trap every four weeks and preserved in 70% alcohol. All beetles sampled in these traps were sorted and identified to morphospecies in laboratory by authors and some taxonomic experts (listed in acknowledgements). Staphylinids of the subfamily Aleocharinae were excluded from analyses because reliable taxonomic keys or catalogue are unavailable.

The definition of saproxylic beetle species is mainly according to Speight (1989) and Alexander (2008). The trophic guilds of saproxylic beetles were identified based upon existing literature or observational records. However, because of the poor taxonomic and biological knowledge of saproxylic beetles in the studied regions, we considered beetles to be in certain guild if they belonged to a group in which most members are in the same guild. Even so, the trophic guild for some beetle species associated with dead wood habitat are still difficult to be ascertained. These species were expediently categorized into 'uncertain' and only occupied less

than 5% of total collected species in our survey.

2.3 Survey of CWD characteristics

In order to reveal the possible influence of environmental characteristics on saproxylic beetle assemblages, we surveyed five CWD variables in a circular plot (10 m in radius, 0.0314 ha) around each sampled snags.

CWD number: The number of coarse wood debris (CWD) with diameter > 10 cm and at least 50% of body falling into the surveyed circular plot were counted.

CWD diameter: The average diameter of CWD in the surveyed circular plot was recorded (at breast height for snags height > 1.5 m; at median height or length for rest snags and logs).

CWD diversity: To calculate the diversity of dead wood (Shannon-Wiener index) in surveyed plots, characters of each CWD were firstly combined into a number including tree species, decay stages (4 stages), diameter classes (10 – 20 cm; 20 – 30 cm; 30 – 40 cm; > 40 cm) and position (snag or log). Then, the diversity of dead wood was calculated as the number of different types of trees in each surveyed plots (Hottola and Siitonen, 2008). The classification of CWD decaying stages mainly follows Wu *et al.* (2008): Stage I, bark remains complete and covers all the log surface except for broken part, wood not softened; Stage II, bark to some extent decayed but with at least 50% remaining, wood softened and could be penetrated 1 – 2 cm in wood with blade; Stage III, bark more decayed and with 25% – 50% remaining, wood extensively softened and could be penetrated 3 – 5 cm in wood with blade; Stage IV, bark almost completely decayed and with < 25% remaining, wood decayed or decomposed.

CWD volume: The volume of CWD in surveyed plot was also calculated. The height of tall snags was estimated by an Altimeter (CGQ-1, Harbin Optical Instrument Factory). The volume of both logs and snags with height < 1.5 m were estimated by Huber's formula: $V = L\pi d^2/4$ (V = dead wood volume, L = length of log or height of snag, d = mid-diameter of log or snag). The volume of unbroken snags is estimated by the formula: $V = aDBH^bH^c$ (DBH = diameter at breast height, H = height of snag). Parameters a, b and c in different tree species referred to the binary tree volume table of Zhejiang province established by Mao (1988). The volume of broken snags was calculated according to the formula: $V = A_bH$ (A_b = basal area, H = snag height).

Snag DBH: The diameter at breast height (DBH) of each cedar snag selected for beetle trap was measured.

Besides five CWD characteristics mentioned above, the canopy cover in each sampled plot was also estimated in our survey because of its possible influence on saproxylic assemblage which has been frequently suggested in temperate forests (Lindhe *et al.*, 2005; Brunet and Isacsson, 2009b). The canopy cover was photographed in the plot center while a digital camera (used in automatic mode) was kept in a vertical position. The canopy images were first converted to black and white model, then the percentage of black (canopy) and white (sky) pixels was calculated (Korhonen *et al.*, 2006).

2.4 Statistical analysis

The nonparametric Kruskall-Wallis and Mann-Whitney *U* test were used to evaluate the statistical significance of difference in stand type means of stand characteristics and beetle data. Spearman's rank correlation was used to analyze the correlation between environmental characteristics and saproxylic beetle data. Crosstabs using Pearson Chi-square were used to test the differences in proportion data of treatments. All these analysis were done in SPSS 13.0 for windows (SPSS Inc., Chicago, IL, USA).

Sample-based rarefaction curves were used to estimate the cumulative number of species with increasing sample number using software package EstimateS 8.0 (Colwell 2006).

The canonical correspondence analysis (CCA) was conducted to explore the correlation of assemblage composition with environmental variables by the software package PC-ORD 5.31 for Windows (McCune and Mefford, 2006). In order to reduce the bulk and noise in our data, only beetle species captured in two or more traps were included in the abundance matrix for this ordination analysis. Prior to this analysis, beetle abundance data were $\lg(x+1)$ transformed to improve distributional normality. Such environmental variables were also lg transformed to meet assumptions of normality as CWD volume, CWD number, CWD diameter, and Snag DBH. The percent data of Canopy cover were arcsine squareroot transformed. The significance of the ordination axes was tested with a Monte Carlo permutation test with 999 permutations. Multi-response permutation procedure (MRPP) was used to test whether saproxylic beetle assemblage differed between stand treatments. Indicator species analysis (Dufrêne and Legendre, 1997) was performed to determine association of particular species with forest types. Species with more than 4 individuals and indicator value (IndVal) greater than 50, whose

statistical significance ($P < 0.05$) was assessed by Monte Carlo randomization test based on 1 000 permutations, were considered as indicators for a forest type. These analyses were also performed on PC-ORD.

3 RESULTS

3.1 Saproxylic beetles sampled and taxonomical composition

In total, 1 429 individuals belonging to 224 saproxylic beetle morphospecies in 44 families were collected from 25 traps. The Staphylinidae predominated with 39 species. Other prominent families were Curculionidae (23 spp.), Elateridae (17 spp.), Nitidulidae (14 spp.), Tenebrionidae (11 spp.), and Scydmaenidae (10 spp.).

Of these species, 52% species were represented by a single specimen. One bark beetle species *Xyleborus saxeseni* accounted for an extraordinarily high proportion (39.5%) of the total beetle individuals. The next two most abundant species were cucujid beetle *Notolaemus* sp. (4.0%) and erotylid beetle *Dacne picta* (3.4%).

3.2 Species richness and abundance

The species number of beetles captured per trap significantly varied amongst forest types (χ^2 = 14.34, $P < 0.001$) (Fig. 1). Both SNMF and YPF had greatly higher species number than MPF. The average number of individuals also greatly varied (χ^2 = 20.47, $P < 0.001$). Over the entire sampling period, the traps in SNMF collected average 97.4 beetle individuals, which was 4.5-fold higher than that collected in MPF. The number of beetle individuals in YPF was significant higher than that in MPF as well.

According to species accumulation curves (Fig. 2), the high overlap of confidence intervals of overall species number indicated that there was no distinct difference in species richness between YPF and SNMF. However, species richness in MPF was significantly lower than in YPF and SNMF.

3.3 Correlation to environmental characteristics

All environmental variables, except for CWD diversity, significantly varied among forest types (Table 1). CWD diameter was the smallest in YPF (χ^2 = 12.04, $P = 0.002$). In contrast, the CWD number in YPF was more than 2.5 times as high as those in SNMF and MPF (χ^2 = 7.84, $P = 0.02$). Accordingly, the CWD volume in YPF was not significantly lower than in SNMF. The lowest CWD accumulation was present in MPF. Compared with SNMF and MPF, YPF had significantly lower canopy cover (χ^2 = 8.47, $P = 0.014$). The DBH of sampling snags was significantly larger in SNMF than in YPF and MPF (χ^2 = 18.54, $P < 0.001$). Additionally, although the variation of CWD diversity among treatments was not supported by Kruskal-Wallis test, the difference between YPF and MPF was still significant (Mann-Whitney U-test, $Z = -2.2$, $P = 0.028$).

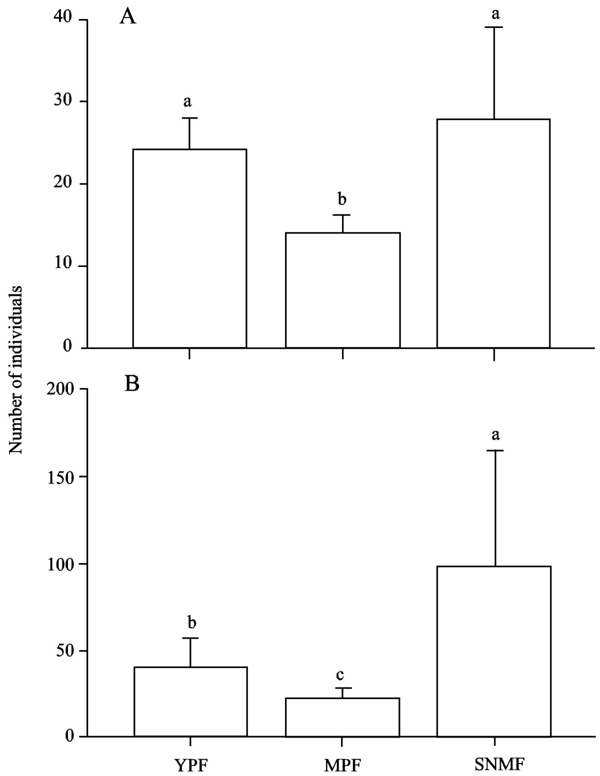

Fig. 1 Number of saproxylic beetle species (A) and individuals (B) captured by flight intercept traps (FITs) in three forest types Data in the figure are means ± *SD*. YPF: n = 7; MPF: n = 8; SNMF: n = 10). Bars with different letters are significantly different at the 0.05 level based on Mann-Whitney U test.

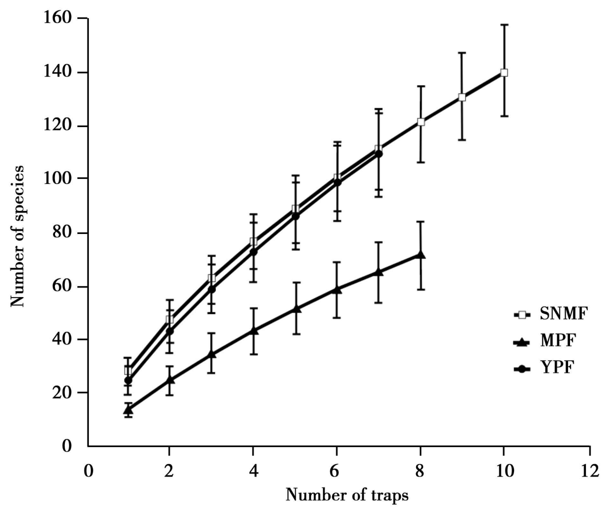

Fig. 2 Sample-based rarefaction curves comparing species density (Mao Tao with 95% confidence intervals) between different forest types

Table 1 CWD characteristics and canopy cover in sampled plots of three forest types, and their correlations with the numbers of species and individuals of saproxylic beetles captured per trap

Environmental characteristics	Forest types			Kruskal-Wallis test		Correlation with saproxylic beetles			
	YPF (n = 7)	MPF (n = 8)	SNMF (n = 10)	χ^2	P	Number of species		Number of individuals	
						Coefficient	P	Coefficient	P
CWD number per ha	559.6 ± 304.3 a	207.0 ± 97.8 b	172.0 ± 87.8 b	7.84	0.020 *	0.14	0.504	−0.24	0.258
CWD diversity	0.85 ± 0.55 a	1.45 ± 0.47 b	1.44 ± 0.45 ab	5.41	0.067	−0.08	0.723	−0.05	0.824
CWD volume (m^3/ha)	78.8 ± 42.2 ab	62.5 ± 42.1 b	193.3 ± 217.5 a	6.30	0.043 *	0.46	0.020 *	0.44	0.026 *
CWD diameter (cm)	18.0 ± 5.7 a	25.6 ± 5.3 b	35.1 ± 11.8 b	12.04	0.002 **	<0.01	0.999	0.36	0.082
Snag DBH (cm)	21.7 ± 5.4 a	27.9 ± 5.6 b	67.9 ± 21.1 c	18.54	<0.001 ***	0.25	0.230	0.61	0.001 ***
Canopy cover (%)	29 ± 27 a	68 ± 18 b	65 ± 20 b	8.47	0.014 *	−0.38	0.059	−0.03	0.903

Data are mean ± *SD*. Kruskal-Wallis test statistics χ^2 value and P value are given. Values in the same row with different letters are significantly different at the 0.05 level based on Mann-Whitney U test. *: $P<0.05$; **: $P<0.01$; ***: $P<0.001$. The same for Table 4. Spearman's rank correlation coefficient and the probability level are given as a measure of correlation between environmental characteristics and the saproxylic beetle data.

According to Spearman's rank correlation analysis, both number of species and number of individuals of saproxylic beetles were significantly related to CWD volume in sampled plots (Table 1). Snag DBH had no significant effect on species richness, but had strong effect on the abundance of individuals ($P = 0.001$). The correlation coefficient between number of beetle individuals and CWD diameter was positive, but not statistically significant. In addition, a marginally significant negative relationship between species richness and canopy cover was also indicated (coefficient = −0.38, $P = 0.059$).

3.4 Assemblage composition

Of species collected in this survey, 140 species were present in SNMF, and 110 and 72 species were present in YPF and MPF, respectively. Seventy seven species were exclusive to SNMF, 50 species were only collected from YPF and 24 species were only captured in MPF. The percent composition of exclusive species were significantly different in three forest types ($\chi^2 = 9.10$, $P = 0.011$). Both SNMF (55.0%) and YPF (45.5%) had higher proportion of exclusive species than MPF (33.3%). Only 25 species (11.2%) were present in all three forest stands (Fig. 3). The number of species shared by any two forest types was generally small (10 − 25 spp.).

Excluding species occurring less than twice in FITs, 97 species were used for CCA analysis. According to the CCA analysis, species assemblages in different forest types were well separated from each other along ordination axes (Fig. 4). The ordination axis 1 and 2 together explained 13.1% of the total variation (Table 2). The first axis represented statistically significant gradients according to Monte-Carlo tests (999 runs, $P = 0.009$). The environmental biplot showed snag DBH, CWD diameter, CWD number and canopy cover were the four most important environmental variables and mainly correlated with the first ordination axis (eigenvalue 0.302).

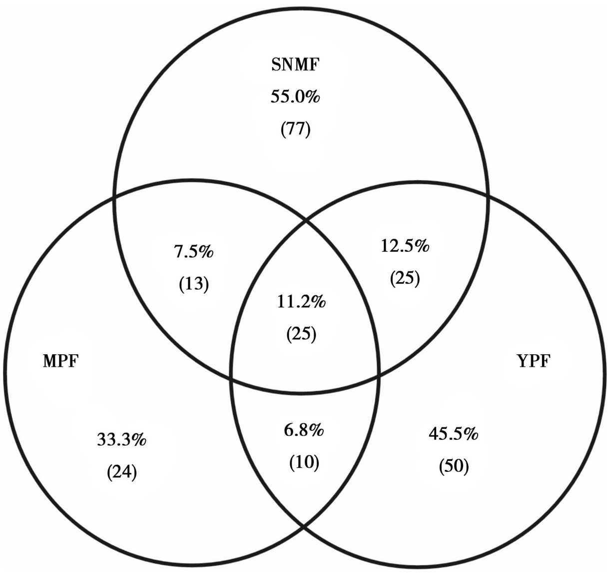

Fig. 3 Venn diagram showing the proportion and number (in parentheses) of exclusive and shared species for each forest type
The percentages for exclusive species were calculated using the number of species of the respective forest type. The percentages of shared species were calculated using either the combined sample of two forest types or all three forest types for the number of species shared between the three forest types.

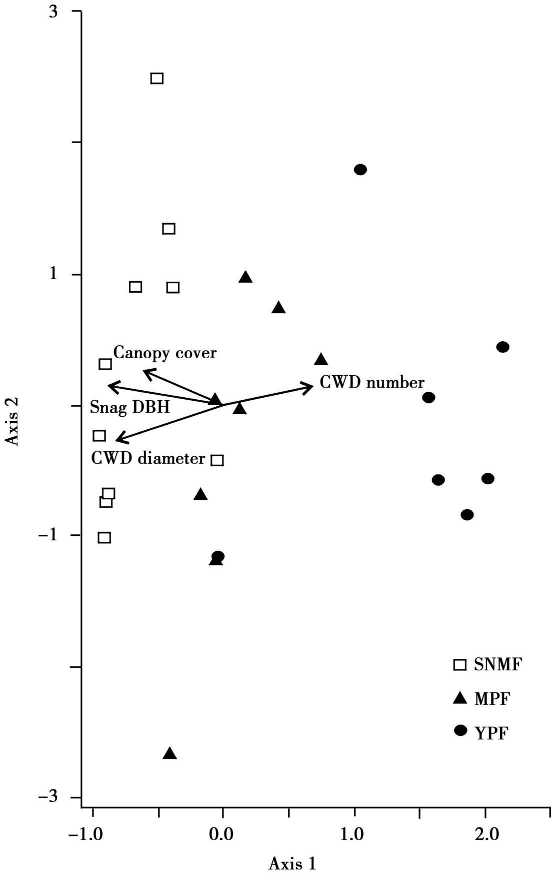

Fig. 4 Canonical Correspondence Analysis (CCA) ordination plot (first two axes) for saproxylic beetles from 25 flight intercept trap samples in three forest types

CCA is based on a matrix of $\lg(x+1)$ transformed beetle abundance data, for species captured by two or more traps (n = 97 spp.). The vector lengths and directions of the environmental variables are shown. Summary statistics are the same as in Table 2.

Table 2 Summary statistics of the first three CCA axes of the CCA performed with a main matrix of the $\lg(x+1)$ transformed numbers of beetles collected by FITs and a second matrix of six environmental variables

Canonical axis	1	2	3
Eigenvalue	0.302	0.221	0.200
Cumulative variance % explained	7.5	13.1	18.0
Pearson correlations species-environment	0.939	0.965	0.940
Inter-set correlations of environment variables			
CWD number	0.660	0.142	−0.151
CWD diversity	−0.291	0.226	0.144
CWD volume	−0.332	−0.239	−0.561
CWD diameter	−0.770	−0.266	−0.120
Snag DBH	−0.826	0.139	−0.399
Canopy cover	−0.584	0.255	0.525

The MRPP analysis supports the ordination results. There were extremely significant differences in species assemblages related to three forest types (Euclidean distance measure, $A = 0.11$, $P < 0.001$). Pairwise comparisons also showed that the difference of assemblages between any given pair of forest types was also extremely significant ($P < 0.001$) (YPF *vs.* MPF: $A = 0.05$; YPF *vs.* SNMF: $A = 0.10$; MPF *vs.* SNMF: $A = 0.10$).

Based on the indicator species analysis, nine and three species were found significantly associated with SNMF and YPF, respectively (Table 3). Only one species in MPF met the indicator standard so it was adopted in our study. It was apparent that more saproxylic

Table 3 Saproxylic beetles with a preference to different forest types according to indicator species analysis

Family	Species	Group	IndVal	*P*	Abundance	Trophic guild
Curculionidae	*Xyleborus saxeseni* (Ratzeburg)	SNMF	79.5	0.001	565	MYC
Curculionidae	*Xyleborus glabratus* Eichhoff	SNMF	70.0	0.001	33	MYC
Curculionidae	*Dryocoetes hectographus* Reitter	SNMF	60.3	0.015	21	PXL
Staphylinidae	*Scaphisoma* sp01.	SNMF	74.2	0.002	30	MYC
Staphylinidae	*Euconnus* sp01.	SNMF	52.7	0.010	15	PRD
Cryptophagidae	*Atomaria* sp01.	SNMF	66.4	0.004	47	MYC
Elateridae	*Cardiotarsus* sp.	SNMF	60.0	0.008	7	PXL
Mycetophagidae	*Litargus* sp.	SNMF	50.0	0.011	5	MYC
Lathridiidae	*Enicmus* sp01.	SNMF	48.3	0.022	20	MYC
Curculionidae	*Xyleborus emarginatus* Eichhoff	MPF	50.0	0.011	6	MYC
Histeridae	*Tribalus* sp.	YPF	82.1	0.001	15	PRD
Cucujidae	*Notolaemus* sp.	YPF	64.0	0.004	57	MYC
Nitidulidae	*Urophorus* sp01.	YPF	50.1	0.008	6	SPF

The significance of observed indicator value (IndVal) is tested by Monte-Carlo randomization test (1 000 permutations). Species with $P < 0.05$, indicator value ≥ 50 and more than 4 individuals are shown. MYC: Mycetophagous; PXL: Phloeoxylophagous; PRD: Predaceous; SPF: Sap-feeder.

3.5 Guild composition

In the comparison of the feeding guild compositions between different treatments were also compared (Table 4), we found that mycetophagous species occupied the highest proportion of the total species richness in each forest type (42.1% - 43.6%), while only very few detritivores were trapped from three forest types. The number of species of mycetophages and phloeoxylophages significantly varied among different forest types ($\chi^2 = 14.22$, $P = 0.001$ and $\chi^2 = 7.07$, $P = 0.029$). However, the proportions of species in different trophic guilds were not significantly different between forest types.

Table 4 Trophic guild composition of saproxylic beetles collected from three forest types

Trophic guild	Forest type			Kruskal-Wallis test		Percentage (number)			Pearson Chi-square test	
	YPF (n=7)	MPF (n=8)	SNF (n=10)	χ^2	P	YPF	MPF	SNMF	χ^2	P
Species										
Mycetophagous	11.4 ± 2.07 a	6.8 ± 1.9 b	13.3 ± 4.9 a	14.22	0.001 **	43.6 (48)	43.1 (31)	42.1 (59)	0.06	0.972
Phloeoxylophagous	4.0 ± 2.9 ab	3.0 ± 1.3 a	6.9 ± 3.5 b	7.07	0.029 *	19.1 (21)	22.2 (16)	28.6 (40)	3.19	0.203
Predacious	5.4 ± 2.4 b	2.9 ± 1.0 a	4.9 ± 2.8 ab	5.03	0.081	23.6 (26)	23.6 (17)	20.0 (28)	0.61	0.739
Detritivore	1.6 ± 0.5 a	0.6 ± 0.9 b	1.6 ± 1.1 ab	5.24	0.073	6.4 (7)	4.2 (3)	4.3 (6)	0.69	0.708
Others	1.9 ± 1.4 a	0.8 ± 1.2 a	1.2 ± 0.9 a	3.54	0.170	7.3 (8)	7.0 (5)	5.0 (7)	0.63	0.729
Individuals										
Mycetophagous	24.4 ± 16.9 a	12.0 ± 4.9 b	77.5 ± 56.3 c	17.63	< 0.001 ***	61.1 (171)	54.9 (96)	79.6 (775)	70.62	< 0.001 ***
Phloeoxylophagous	4.4 ± 2.6 a	4.8 ± 2.8 a	9.2 ± 5.7 a	4.50	0.105	11.1 (31)	21.7 (38)	9.5 (92)	22.35	< 0.001 ***
Predacious	7.1 ± 4.1 a	3.0 ± 1.2 b	6.2 ± 4.3 ab	4.87	0.088	17.9 (50)	13.7 (24)	6.4 (62)	37.43	< 0.001 ***
Detritivore	1.7 ± 0.5 a	1.1 ± 1.6 a	3.1 ± 3.0 a	4.19	0.123	4.3 (12)	5.1 (9)	3.2 (31)	2.04	0.360
Others	2.3 ± 1.7 a	1.0 ± 1.6 a	1.4 ± 1.1 a	3.27	0.195	5.7 (16)	4.6 (8)	1.4 (14)	18.19	< 0.001 ***

Data for comparison of beetle species and number of individuals are mean ± *SD*. Other categories here include sap-feeder and groups with uncertain trophic guilds.

As far as the abundance of individuals was concerned, more than 70% of beetle individuals were mycetophagous, and only the number of individuals of mycetophagous guild was significantly different between forest types ($\chi^2 = 17.63$, $P < 0.001$) (Table 4). However, the proportion of individuals in different guilds, except for in detritiveores, significantly varied among forest types. This result was not consistent with the comparative result of species proportions, and could be greatly affected by a few dominant species that exhibit different preference for different forest types.

4 DISCUSSION

4.1 Variability of CWD characteristics

The great change of amount, structure and dynamic of CWD in managed forests has been widely reported (Linder and Östlund, 1998; Kirby *et al.*, 1998; Fridman and Walheim, 2000). The quantitative and qualitative patterns of CWD in planted forests were also proposed in some studies (Green and Peterken, 1997; Matthew and Grigal, 1999; Brin *et al.*, 2008). Generally, these studies revealed a sharp decline of CWD amount in managed and plantation forests. However, in the present study, the average CWD volume in YPF is relatively high and almost reaches 80 m^3/ha, and is even greater than that in MPF (ca. 64 m^3/ha), and beyond 40% of these natural levels. The increase of CWD accumulation in YPF cannot be attributed to anthropogenic disturbance because this forest stand had not experienced any productive activities since it was planted 30 - 40 years ago. Thus, the natural disturbance is the only explanation for the creation of CWD in YPF. It is observed in field that young Chinese cedars with small diameter and high stand density are more easily broken during a heavy snow in winter. The significant high CWD number in YPF is the other good evidence for this snow damage. In contrast, cedars in mature plantation forest are strong enough and less vulnerable to the snow-breakage. Snow damage not only creates large amounts of CWD, but also creates canopy openings in YPF. That is why the canopy cover is significantly lower in YPF than those in SNMF and MPF. Therefore, snow damage plays an important role in constructing CWD habitats in cedar plantations. There is no reason to

confer that the CWD accumulation in young plantation forests should be lower than old growth forests, without considering the different creation mechanisms of CWD in different climatic regions.

However, despite with high number of CWD, YPF actually fail to provide a high heterogeneous substrate for saproxylic fauna. The monospecific plantation and less varied decay stage of CWD are important causes of the decrease of CWD diversity index in YPF. Furthermore, the comparison of CWD diameter also indicates that CWD of large size are more common in mature and semi-natural forests. The significant difference in diameter of sampled cedar snags was also detected. Although these sampled cedar snags only occupy very small part of snags in each stand, they may represent the truth that most Chinese cedars in natural forest always have relative large diameter. The severe intra-specific competition and extremely low population renewal rate are two possible mechanisms to explain why Chinese cedars easily grow into large diameter in natural conditions (Zhang *et al*., 2004).

4.2 Species richness and abundance

The negative influence of intensive forest management on species richness of saproxylic beetles has been widely reported, whereas the opposite trend was also present in some studies. For example, it was proposed that a managed forests in central Finland hosted a higher number of species of saproxylic beetles than primeval forest (Väisänen and Biström, 1993). Kaila *et al*. (1997) also found a higher expected number of species of saproxylic beetles in clear cut forests than in closed mature forest.

In the present study, no significant differences in species richness of saproxylic beetles were detected between YPF and SNMF. Contrarily, the lowest number species was present in MPF. The similar trend also existed in beetle abundance. Thus, environmental characteristics in studied sites may have more important effects on species richness and abundance than management history. Amongst six environmental variables measured in our study, CWD volume was found to have significantly positive effects on both species richness and abundance. Similar results were also present in many previous studies (Martikainen *et al*., 2000; Similä *et al*., 2002a; Müller *et al*., 2008). Thus, the CWD volume can be treated as a better predictor for species richness of saproxylic beetles in subtropical forests or Chinese cedar dominated forests.

It is little unexpected that average CWD diameter in our study has less effect on species richness and abundance of saproxylic beetles. In many studies, the diameter of CWD has been identified as an important factor for predicting the species richness of saproxylic beetles and occurrence of many saproxylic species (Siitonen, 2001; Grove, 2002a; Similä *et al*., 2003). It was concluded that large dead wood can provide more heterogeneous habitats and more stable microclimate for many species, and support more species of fungi (Grove, 2002a). However, the inconsistent results were also present in some studies. Jonsell *et al*. (2007) found that differences in species richness of saproxylic beetles between diameter classes were minor for different tree species. Schiegg (2001) ever suggested that limbs of beech hosted more species of saproxylic insects than trunks. In our study, the effect of CWD diameter was probably underestimated at a small spatial scale. However, correlation analysis between snag DBH and species richness of saproxylic beetles also did not support that large dead wood is better in sustaining species richness of saproxylic beetles. However, on the other hand, beetle abundance, in our study, was significantly correlated to snag DBH. This result hints that large snags of Chinese cedar possibly play important roles in sustaining stability of saproxylic beetle population in natural subtropical forests. Thus, the value of large diameter CWD in sustaining integrity of saproxylic beetle community should further debate.

Except for CWD diameter, CWD diversity in our study is also found to have a very weak influence on species richness. It is possible that high diversity is not equal to high quality. For example, it is observed that CWD in MPF plots are frequently more decayed than those in YPF, probably due to lack of constant supply of fresh deadwood. Saproxylic beetle species may be less abundant on these CWD in later decay stages (Jonsell *et al*., 1998; Wu *et al*., 2008).

With respect to canopy cover, the negative correlation between canopy cover and number of species in our study is marginally significant ($P = 0.059$). However, in one recent study (Wu *et al*., 2013), the negative effect of canopy cover on number of beetle species associated with different tree species snags is strong and significant. In temperate forests, sun exposure has also been clearly suggested to be an important factor for the distribution of saproxylic beetles (Kaila *et al*., 1997; Sverdrup-Thygeson and Ims, 2002; Horák *et al*., 2012). Thus, the significantly lower canopy cover may be one explanation for the high species richness in YPF. The effect of sun exposure also

should be fully considered in conservation of saproxylic beetles in subtropical forests.

4.3 Assemblage composition

Many studies have suggested that composition of saproxylic beetle assemblages could be greatly changed by forest management practices (Martikainen *et al*., 2000; Similä *et al*., 2002b; Dollin *et al*., 2008). In the present study, species assemblages were clearly different between forest types. Even between young and mature plantation forests, beetle assemblage was distinctly different. According to the CCA analysis, at least four environmental variables measured in our study have marked influences on assemblages (Fig. 2). The diameter sizes of both CWD in surveyed plot and sampled cedar snag were showed to be most crucial to the composition of beetle assemblages. It seems that CWD diameter has a more distinct effect on assemblage composition than on species richness of saproxylic beetles. The deadwood diameter may be more important in predicting occurrences of saproxylic species specific to certain diameter class of dead wood (Nordén and Paltto, 2001; Grove, 2002a; Brin *et al*., 2011). Additionally, the positive correlation between the amount of CWD and the heterogeneity of CWD habitats (not equal with diversity index in our study) has been proposed in some studies (Müller and Bütler, 2010; Janssen *et al*., 2011). It is possible that CWD density may have an important effect, which could not be substituted by the effect of CWD volume, on the distribution of certain saproxylic beetle species. The marked influence of canopy cover or sun-exposure on assemblage composition is in line with previous studies (Kaila *et al*., 1997; Brunet and Isacsson, 2009b). The great influence of forest canopy cover on species composition in Chinese cedar will have a positive meaning for the conservation of saproxylic beetles in Chinese cedar dominated forests.

Indicator species analysis showed that 9 species were significant indicators of the SNMF. Relatively, only very few species could be considered as indicators of YPF and MPF. This result suggests that SNMF stands have more stable or distinctive habitat features and are therefore important for colonization of many saproxylic beetle species. Among these indicator species, the bark beetle species *X. saxeseni* is predominant in all three forest types, and shows a significant preference to SNMF. It is known that this bark beetle species is widely associated with both coniferous and broad-leaved hosts (Yin *et al*., 1984). Thus, besides environmental characteristics surveyed in our study, the high tree species diversity in SNMF may also have strong effects on distribution of saproxylic beetles.

4.4 Guild structure

Besides influencing assemblage composition, forest management also could change the trophic guild structure of saproxylic insects. For example, old-growth forest tended to be richer in detritivores, mycophages and predators than re-growth and logged forests (Grove, 2002b). Xylophagous and fresh dead wood inhabiting species had a higher number of individuals in intensively managed forests that offer a high amount of fresh dead wood by logging than strict forest reserve (Müller *et al*., 2008). In the present study, although the number of species of mycetophage and phloeoxylophage significantly differed, the proportion of species in different guilds was almost consistent in different forest types. Thus, no guilds tended to be proportionately richer in species in one of three forest types. At present, both the beetle sampling method and the tree species selected in our study make it difficult to compare our results with other studies. However, the significantly higher proportion of individuals of mycetophage in SNMF implied that forest plantation might truncate the food chain of saproxylic beetles based on fungi. It was consistent with the result of indicator analysis that more mycetophagous species significantly preferred to colonize on snags in SNMF. However, we still knew little about the biological relationship between saproxylic beetles and fungi in subtropical forest. The related studies should be greatly improved in the future.

5 CONCLUSION AND MANAGEMENT IMPLICATIONS

Our study suggests that young cedar plantation forest also can harbor high number of species of saproxylic beetles due to the great amount of CWD and high sun-exposed habitats created by natural disturbance. Thus, we agree with the view that habitat factors (structure) *per se* were better predictors for saproxylic beetle species richness than management history or intensity (Müller *et al*., 2008). However, the significantly lower number of species in mature cedar plantation forest indicates that species richness in young cedar plantation forest may decline in later succession stage. Thus, the long term effect of Chinese cedar forest plantation on the species richness of saproxylic beetles should not be optimistic. Furthermore, our results also suggest that, even if the amount of decaying wood in plantation forests could be increased to the level

observed on our study sites, saproxylic beetle assemblages in cedar plantation forests would still be clearly different from semi-natural forests. The large-diameter CWD pieces in SNMF are probably important for species composition of saproxylic beetles. Thus, cedar plantation forests are clearly less valuable in maintaining or restoring the natural integrity of subtropical forest biodiversity.

In China, plantation forests have been used as an important measurement to restore the degraded forest and lands. Our study may be enlightening for making the forest plantation plan in subtropical China. For preserving saproxylic fauna, retaining the natural tree species composition during the plantation of forest is obviously better for long-term persistence of saproxylic fauna than single species plantation. For existent plantation forests, the current policy of forest conservation that prohibits any forms of anthropogenic disturbance should be greatly changed. Both our and many previous studies have identified the CWD volume as a better predictor for saproxylic beetle diversity. Thus, it is appropriate to emulate natural disturbance in nature reserve region to increase continuity of the quantity of dead wood in plantation or secondary forests. It is also technologically feasible to use CWD volume to quickly assess the species richness of saproxylic beetles in plantation forests. No matter what kind of measurement we take, the natural forest conservation and the habitat requirement of saproxylic insects should be considered in priority.

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浙江天目山种植林管理历史及粗死木残体特征影响柳杉腐木甲虫多样性

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摘要：不合理的森林管理是导致腐木甲虫多样性丧失的重要原因。在中国亚热带地区，多样性较高的天然林已被大面积的人工种植林取代，然而，这些人工林对腐木甲虫多样性的影响还研究甚少。本研究对浙江天目山自然保护区人工幼龄林(30 ~40 年)、人工老熟林(80 ~100 年)和半天然混合林(>200 年)中柳杉枯立木上的腐木甲虫群落及多样性进行比较。结果表明：半天然混合林腐木甲虫个体数量(97.4 ±66.7)显著高于幼龄林(39.9 ±16.3)和老熟林(21.9 ±5.9)，但半天然林混合林(27.9 ±11.2)与幼龄林(24.1 ±3.7)腐木甲虫物种数差异并不显著($P >0.05$)，而幼龄林的腐木甲虫物种数和个体数量则显著高于老熟林($P <0.05$)。腐木甲虫物种数和个体数量与样地粗死木残体体积相关性显著($P <0.05$)。典范对应分析和多响应置换过程分析表明腐木甲虫群落特征在不同林型间差异显著($P <0.001$)。柳杉枯立木直径、粗死木残体的直径和数量以及林冠盖度均对腐木甲虫物种组成具有显著影响($P <0.05$)。腐木甲虫营养级组成分析也表明，半天然混合林菌食性甲虫数量显著高于种植林($P <0.001$)。结果提示，提高种植林粗死木残体的数量和质量可以增加腐木甲虫的物种丰富度，但种植林腐木甲虫多样性可能在随后的演替阶段有所下降，而且种植林与天然林在腐木甲虫群落组成上差异十分明显。

关键词：腐木甲虫；物种多样性；柳杉；管理历史；种植林；粗死木残体；天目山

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